EFFECTS OF TEMPERATURE, SALINITY, AND SUBSTRATUM ON LARVAE OF THE SHIPWORMS *TEREDO BARTSCHI* CLAPP AND *T. NAVALIS* LINNAEUS (BIVALVIA: TEREDINIDAE)

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ABSTRACT

Teredo bartschi Clapp was introduced into the effluent of a nuclear generating station at Oyster Creek, New Jersey, in 1974. Normally it maintains breeding populations in Florida and the Caribbean Sea. This species releases pediveliger larvae, capable of swimming and crawling prior to permanent attachment to wood. Field collections of pediveligers were made in the vicinity of Oyster Creek. Laboratory studies compared survivorship and behavioral patterns of pediveligers of *T. bartschi* and veligers and pediveligers of *T. navalis* Linnaeus under various environmental conditions. The purpose of the study was to contrast *T. bartschi* with the native shipworm *T. navalis* Linnaeus, which releases young in the straight-hinge veliger stage.

Pediveligers of *Teredo bartschi* were active between 16-32ºC and 6-35 $^0/_{00}$ salinity, whereas pediveligers of *T. navalis* were active between 10-29ºC and 6-31 $^0/_{00}$. In both species, pediveligers could not tolerate as high a salinity or as low a temperature as adults. At 5 $^0/_{00}$, pediveligers of both species died. As salinity was reduced, pediveligers of *T. bartschi* exhibited a greater tendency to probe wood and burrow. This behavior could be an adaptation in mangrove or estuarine habitats allowing settlement on wood in the mid-range of the salinity gradient.

During the breeding season, pediveligers of *Teredo bartschi* were not often found far from wood and adults, yet the pediveligers do not settle preferentially on wood already containing adults. Clustering of pediveligers causes a highly patchy distribution of adults. Species that release pediveligers have high survivorship and high probability of finding suitable substratum as long as that substratum is abundant and renewable, as it is in tropical mangrove environments.

In 1974, the subtropical shipworm *Teredo bartschi* Clapp was found living and breeding in the heated effluent and marginal areas receiving heated water from the Oyster Creek Nuclear Generating Station, Barnegat Bay, New Jersey (Turner, 1974). It was presumed that this species had been introduced from Florida or another southern locality (Hoagland and Turner, 1980). *Teredo bartschi* has not been found breeding in natural-temperature waters north of Cape Hatteras, but it has been found breeding in the thermal effluent of the Millstone nuclear power plant in Connecticut (Battelle Columbus Laboratories, 1979).

Native species of shipworms in Barnegat Bay are *Bankia gouldi* (Bartsch) and *Teredo navalis* Linnaeus. Larval development of *B. gouldi* occurs entirely in the plankton, whereas *T. navalis* maintains larvae in a brood pouch in the gills until the straight-hinge stage is reached (Culliney, 1975). *Teredo bartschi* also broods its young, but retains them longer until the pediveliger stage is reached (Hoagland, 1983a). Although pediveligers of *T. bartschi* have a well-developed foot and are capable of settling and burrowing almost immediately upon release, they often spend several days alternately crawling and swimming before finally settling and excavating a burrow.

Once *Teredo bartschi* was introduced to Barnegat Bay, it became a potential competitor of native species for the limited wood substratum available. Relative abilities of the larvae and pediveligers to survive and settle under different physical conditions within and outside the thermal effluent at Oyster Creek were of interest. Experiments described in this paper were performed to delimit the abilities of pediveligers of *Teredo bartschi* to survive and metamorphose under a series of temperatures, salinities, and substratum conditions. Whenever possible, data were obtained on straight-hinge veligers and pediveligers of *T. navalis* for comparison.

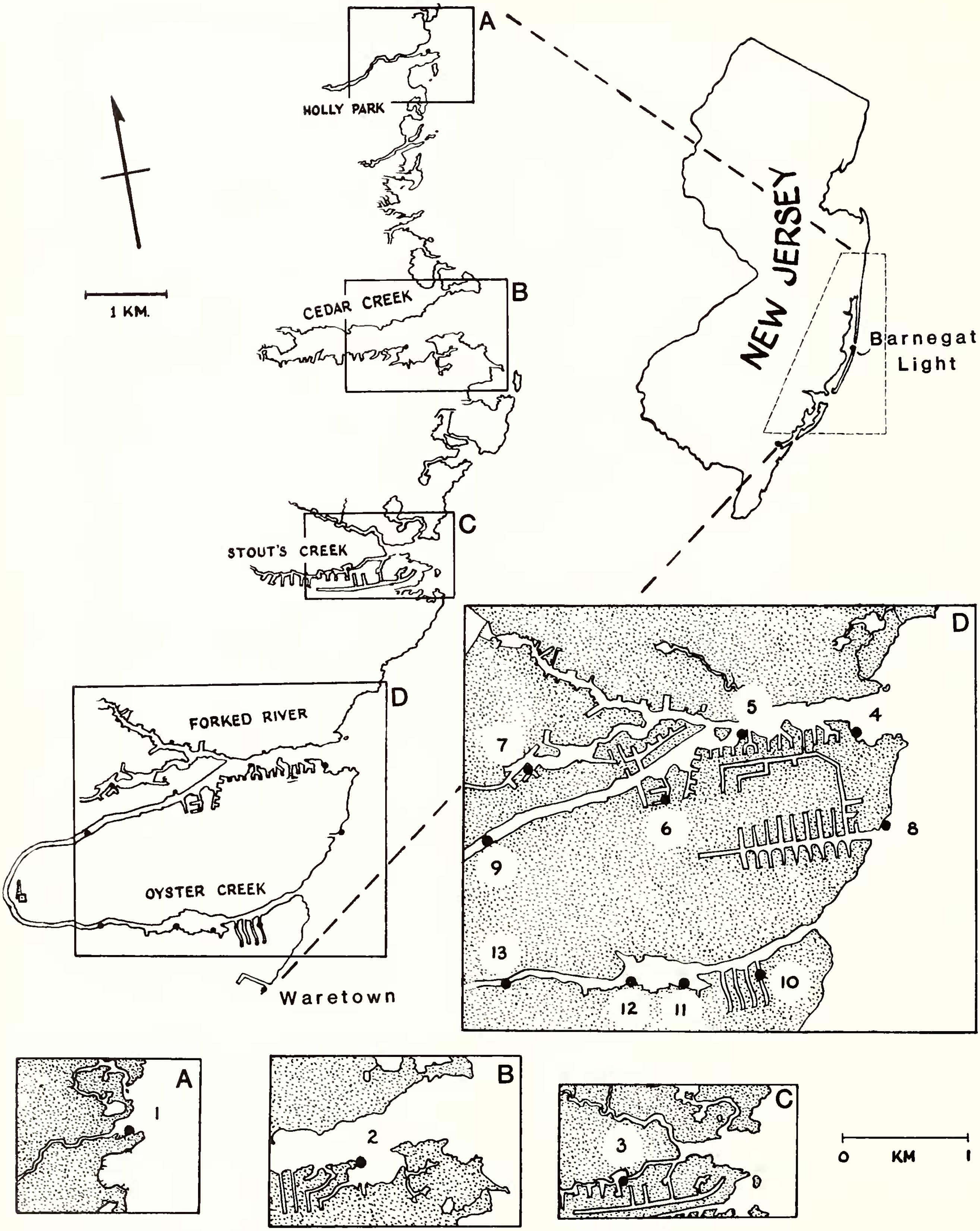

Fig. 1. Map showing the area of study in Barnegat Bay, New Jersey, and its location on the New Jersey coast.

METHODS

White pine panels were used to collect shipworms in Oyster Creek, Forked River, and nearby portions of Barnegat Bay as far south as Barnegat Light between 1976 and 1982 (Fig. 1). Water temperature and salinity were recorded monthly at each collection site. Panels were collected, X-rayed, then dissected to remove shipworms each month. The settlement of larvae was estimated from numbers in panels left in the water 1 month, and the percentage of adults brooding larvae was calculated from dissection of adults taken from panels left in the water 6-12 months.

Live teredinids were obtained from the panels for physiological studies in 1979-1982. Pure cultures of *Teredo navalis* were obtained from Long Beach Island near Barnegat Light (Fig. 1). Panels removed from Oyster Creek in May and in October-November contained pure cultures of *T. bartschi*. The panels were returned to the laboratory once they had become infested with shipworms. After scraping to remove fouling organisms, the panels were placed in holding tanks of 22-24 $^0/_{00}$ salinity and a temperature of about 24 ± 3^{0}C (close to late spring and summer conditions at the collecting sites). Larvae released in aquaria by *Teredo bartschi* and *T. navalis* were collected on Nitex screen sieves and used in salinity and temperature-tolerance experiments. The larvae were fed cultures of *Monochrysis lutheri* and *Isochrysis galbana*. The procedures for culturing shipworms are described in Turner and Johnson (1969), Culliney, Boyle and Turner (1975) and Culliney (1975). Larvae used in experiments were first and second generation, both reared in the laboratory.

A series of temperature and salinity tolerance tests were conducted, lasting from a few hours to several months. Behavioral changes indicated temperature and salinity stress to individual animals. Several types of behavior were categorized for veligers and pediveligers: swimming actively or slowly near the bottom, crawling on a wood sliver or on the culture dish, probing the wood, beginning to bore, pulsating on the culture dish bottom, closed on the bottom, or swollen open and inactive on the bottom. The last two behaviors were indicative of suboptimal conditions if observed with greater frequency than in controls. In each experimental trial, at least 10 juveniles were held per culture dish per experimental trial; most experiments were replicated. The difference in behavior between experimental animals and controls (at fixed temperature and salinity) was recorded.

In all cases, controls were manipulated exactly as were experimental containers, including periods of agitation. Experiments were done in noncirculating filtered seawater changed every 2-3 days, so that close observations could be made and temperature and salinity could be controlled. The health of all species and life history stages would likely be better in an open system, but the comparative aspects of the results here are of value. Also, open systems can introduce unwanted predators.

The following experiments were performed with new animals for each trial; the number of trials per experiment varied and are given with the results. Statistical analyses for comparing results included the chi-square contingency test and Mann-Whitney U-test, as appropriate.

1. SALINITY CHANGE

Pediveligers of both species and straight-hinge veligers of *Teredo navalis* raised at 22 $^0/_{00}$ and 24 ± 3^{0}C were subjected to both rising and falling salinities in separate experiments, 12 pediveligers and 50 veligers per trial, three times in each direction. Salinity was raised gradually from 22 $^0/_{00}$ by adding a concentrated solution of sea salts, a maximum of 3 $^0/_{00}$ per hour. Salinity was lowered at the same rate using dechlorinated fresh water. A pipette-drip system was employed to add water in all experiments, and the containers were aerated to facilitate mixing. The experiment continued until all animals showed stress, with observations made every half hour. The time interval was short because metamorphosis can occur within a few days.

2. RESPONSE TO CONSTANT REDUCED AND RAISED SALINITY

Ten pediveligers per culture dish of *Teredo bartschi* and *T. navalis* were subjected gradually over a 6-hour period at 20-22^{0}C to salinities of 2, 5, 10, 15, 20, 22, 25, 30, 32, 35, 40, and 50 $^0/_{00}$ by dilution or elevation as above. After the target salinities were reached (time zero), observations on behavior were made every 20 minutes for the first 4 hours, then at 6 hours, and then 3 times daily (at salinities 5, 10, 15, 20, 25, 30, and 35 $^0/_{00}$) for 5 days. Two trials were performed.

3. SUDDEN SALINITY CHANGE

Fifteen pediveligers of *Teredo bartschi* per dish at 24^{0}C were subjected to salinity change as above, but more rapidly, either from 22 $^0/_{00}$ to 27 $^0/_{00}$, 22 $^0/_{00}$ to 32 $^0/_{00}$ or 22 $^0/_{00}$ to 12 $^0/_{00}$ over a 2-hour interval. Controls were left at 22 $^0/_{00}$. Observations were made for 15 minutes before and after salinity was changed, and again after it was returned to 22 $^0/_{00}$ over a 2-hour interval.

4. UPPER TEMPERATURE TOLERANCE

While salinity was maintained at 22 ± 1 $^0/_{00}$, temperature was raised 2^{0}C per day, using aquarium heaters. Straight-hinge veligers and pediveligers of the two *Teredo* species were examined, 10 animals per experiment, and behavioral changes were observed over a 5-day period.

5. LOWER TEMPERATURE TOLERANCE

At the constant control salinity, pediveligers of both species were subjected to falling temperatures of 5^{0}C per day and their behavior monitored. Also, *T. bartschi* pediveligers were observed for 5 days at 5^{0}C and at 18-20^{0}C. There were 10-12 animals per test.

6. TEMPERATURE-SALINITY INTERACTION

Pediveligers of *Teredo bartschi* were exposed to 18 identical panels of clear white pine cut from the same board. After the young postlarvae began to bore, they were counted and the panels were isolated from one another in filtered and aerated sea water. Two panels each were established at all

Table 1. Effect of gradual salinity change, *Teredo* species, triplicated. Tabular values are the salinity at which at least 50% of the test individuals were moribund (controls at 22-24 ‰ showed no abnormal behavior). All experiments were performed at temperature = 24 ± 3°C. Sample sizes (N) are in parentheses.

	LOWERED SALINITY ‰				RAISED SALINITY ‰			
Trial:	1	2	3	*Mean*	1	2	3	*Mean*
T. bartschi Pediveligers	7(12)	4(12)	8(10)	6.3	27(12)	35(12)	35(12)	32.3
T. navalis								
Veligers	6(50)	6(50)	—	6	31(50)	27(50)	—	29
Pediveligers	6(12)	6 (12)	—	6	31(12)	—	—	31

combinations of 10, 20, and 30°C and 6, 14, and 22 ‰ salinity.

The water was changed weekly and filtered. The experiment began on 18 February 1981, and was ended on 20 May 1981. Each time the water was changed, it was examined for pediveliger larvae. At the conclusion of the experiment, the panels were X-rayed. The number of specimens per panel and their lengths (mm) were recorded.

7. WOOD PREFERENCE

Behavior of *Teredo bartschi* pediveligers was observed when they were exposed to new wood soaked for 2 weeks in artificial seawater, wood held previously in the field for several months but without shipworms (old wood), and wood from the field containing adult shipworms. Behavioral observations were made after 3 hours, before adults in the wood released additional larvae. Ten individuals were observed on each of four trials. Three behaviors were recognized: swimming, sitting on the bottom of the glass container, or sitting/burrowing on wood.

At the field sites, the distribution of shipworm veligers and pediveligers was observed by taking replicate plankton tows at distances 0-1 m and 2-3 m from the collecting panels. Plankton sampling was done in June, July, October, and November, 1980 and 1981, and in August and September, 1982, in Oyster Creek, Forked River, and Waretown Creek (south of Forked River).

To observe patterns of settlement in the field, white pine stakes 3x7x90 cm were submerged at Forked River, Oyster Creek, and Waretown Creek. Three identical stakes were driven into the mud against the bulkhead at each station, at a slight angle and such that the stakes extended above the water line. The purposes of the experiment were to test the idea that shipworms settle preferentially at the mudline, and to see if the different species have the same settlement preferences. Stations were chosen to maximize the probability of obtaining large sets of all species. One and then two stakes from each station were removed after 4 and 16 months, respectively, and marked as to the orientation of each surface with respect to currents, which were unidirectional in Forked River and Oyster Creek due to operation of the power plant. Mudlines and waterlines were also marked. The stakes were X-rayed and measurements were taken of positions of boreholes, length and direction of growth of burrows. Each individual borer was identified to species.

RESULTS

SALINITY CHANGE

When salinity was raised gradually at 24 ± 3°C, larvae of both *Teredo bartschi* and *T. navalis* withstood salinity higher than found in Barnegat Bay (Table 1). There was no significant difference between species in upper or lower salinity tolerance (Mann-Whitney U-test probabilities >0. 2 and =0.4, respectively), although pediveligers of *T. bartschi* remained active at slightly higher salinity than did larvae of *T. navalis*. Larvae of both species failed to recover once exposed for over 6 hours to 6 ‰, except for one individual pediveliger of *T. bartschi*, which survived for over a month at 24 ‰ after being kept at 4 ‰ for 10 days. It did not successfully bore into wood.

When salinity was between 15 ‰ and 10 ‰, pediveligers of *Teredo bartschi* increased their crawling and boring activity, relative to swimming. At this salinity range, 50% of test animals exhibited burrowing behavior, as opposed to 20% of controls kept at 22 ‰. All forms of activity fell at 10 ‰; below this level, boring ceased. There was no difference between the responses of straight-hinge veligers and pediveligers of *Teredo navalis*. The behavioral change of both species at 6 ‰ was abrupt. Either abnormal swimming or swelling occurred in all individuals when the salinity was held constant at 6 ‰ for 24 hours.

CONSTANT REDUCED AND RAISED SALINITY

Pediveligers of *Teredo bartschi* maintained at constant changed salinity behaved as summarized in Table 2. Behaviors were pooled into three categories, active, stressed (closed, gaping), or dead, to facilitate comparison of the two species. After 6 hours, behavior indicative of stress occurred at about 5 ‰ and below, and at 32 ‰ and above. Changes in behavior of pediveligers occurred over time, with increased boring activity evident after 2 days at 10-32 ‰. Above 35 ‰, all individuals were closed on the bottom or dead. Below 5 ‰, all individuals gaped or died. Those pediveligers that swam at salinities at and below 10 ‰ did so slowly and in circles near the bottom. Between 15 and 30 ‰, swimming was primarily up and down, and the animals were less frequently near the bottom. After 5 days, a few pediveligers maintained in the range of 10-30 ‰ gaped and appeared stressed, but over twice as many gaping

Table 2. Response of pediveliger larvae to constant salinity (accurate to ± 0.5 ‰) at various levels after 6 hours and 5 days. N = 20 per salinity level. Behaviors are summarized as percent S = stressed (gaping or closed), A = active (boring, crawling, swimming, or pulsating on the bottom), or D = dead.

	T. bartschi						*T. navalis*					
	6 h			5 d			6 h			5 d		
Salinity ‰	A	S	D	A	S	D	A	S	D	A	S	D
2	0	100	0	0	0	100	0	100	0	0	0	100
5	80	20	0	20	80	0	70	30	0	25	75	0
10	100	0	0	65	35	0	50	50	0	75	25	0
15	100	0	0	95	5	0	100	0	0	95	5	0
20	100	0	0	90	10	0	100	0	0	95	5	0
22	100	0	0	—	—	—	100	0	0	—	—	—
25	100	0	0	75	25	0	100	0	0	100	0	0
30	100	0	0	95	5	0	100	0	0	100	0	0
32	80	20	0	—	—	—	90	10	0	—	—	—
35	50	50	0	90	10	0	30	70	0	75	25	0
40	0	100	0	0	0	100	0	100	0	0	0	100
50	0	100	0	0	0	100	0	100	0	0	0	100

pediveligers occurred at 5 ‰ than at any of the higher salinities.

Results for *Teredo navalis* pediveligers were similar to those for *T. bartschi*, except that most pediveligers of *T. navalis* were boring within the 5-day period of the experiment, whereas numerous *T. bartschi* remained motile. This observation is consistent with observations of *T. bartschi* in the holding tanks; larvae of *T. bartschi* survived 14+ days as pediveligers prior to successful settlement.

SUDDEN SALINITY CHANGE

Sudden salinity change from 22 ‰ to 27 ‰ and 22 ‰ to 32 ‰ caused all pediveligers of *Teredo bartschi* to close up and fall to the bottom. Only three individuals of 30 regained activity during 15 minutes of observations. However, when returned to 22 ‰, all larvae began swimming within 15 minutes. Sudden lowering of salinity to 12 ‰ caused less abrupt a response, but within 15 minutes all individuals slowed their swimming or fell to the bottom and pulsated (opened and closed the valves). Likewise, recovery time when returned from 12 ‰ to 22 ‰ was slower; only 12 of 30 individuals resumed active swimming in 15 minutes.

UPPER TEMPERATURE TOLERANCE

Fifty percent inactivity of pediveligers of *Teredo bartschi* occurred as the temperature of the test chambers reached 32° and 33°C in two trials, while 83% of controls maintained at 20°C remained active. Complete inactivity occurred at 34° and 35°C, respectively. Pediveligers of *T. navalis* were 50% inactive at 29°C and 100% inactive at 31°C. The length of time the animals were exposed to each temperature influenced the result; had individuals of *T. bartschi* been left longer at 33 °C, they might have all become inactive at that temperature. Comparatively speaking, however, *T. navalis* showed thermal stress at lower temperature than did *T. bartschi.*

LOWER TEMPERATURE TOLERANCE

Half of the pediveligers of *T. bartschi* were inactive at 16°C. Only three of the 24 individuals showed some crawling response after one day at temperatures of 10°C. In controls maintained at 20°C, 83% of the individuals were active after one day. Pediveligers observed for a 5-day period at 5°C showed no activity past the first day, whereas over half of the control animals kept at 18-20°C were active each time observations were made. When returned to 18-20°C, the pediveligers that had been kept at 5°C all failed to penetrate the wood and died, whereas 55% of the control animals metamorphosed. *Teredo navalis* pediveligers were slightly less sensitive to low temperature. Fifty percent of larvae were still active at 10°C.

TEMPERATURE-SALINITY INTERACTION

Pediveligers of *Teredo bartschi* allowed to bore into wood and maintained for three months at several combinations of temperature and salinity showed the earliest maturation at 20°C and 22 ‰ (Table 3). No release of larvae took place at 10°C, and reproduction was delayed at 6 ‰ salinity (20°, 30°C). Greatest growth occurred at 30°C and the two higher salinities, 14 ‰ and 22 ‰, and at 20°C/22 ‰, although growth was variable among individuals and between replicate panels. The optimal combination for both survival and reproduction was 20°C/22 ‰. Mortality was lowest at the intermediate temperature.

WOOD PREFERENCE: LAB STUDIES

Wood preference experiments in the laboratory showed that *Teredo bartschi* pediveligers settled most frequently on new wood not previously used in Oyster Creek (Table 4). They avoided wood taken from the field, even when it contained adults. Clustering of pediveligers as they settled on the wood occurred whether or not adults were present. A X^2 contingency test on data in Table 4 pooling the trials and comparing new wood, old wood, and wood with larvae versus the three locations of larvae gave a value of 51.5 with 4 d.f., significant at $p < .001$. The cells that deviated most strongly from expected frequencies were the number of pediveligers on wood (significantly large when new wood was offered, but smaller than expected on old wood whether or not adults were present) and the number swimming (large when offered wood containing adults; small when offered new wood).

WOOD PREFERENCE: FIELD STUDIES

Settlement patterns of teredinid larvae on wooden stakes in Barnegat Bay are reported in Table 5. After 4 months, it appeared that most larvae of *Teredo bartschi* settled near the mudline; no such trend occurred for the other species. However, stakes removed after 16 months showed no preferred settlement of larvae near the mudline for any species, and no preferred settlement on the protected sides of the stakes (Oyster Creek and Forked River run in one direction due to pumping of water for the Oyster Creek Nuclear Generating Station). There was a strong tendency for pediveligers of *T. bartschi* to settle in clusters, and for *T. navalis* to be scattered along the length of the stakes. Once metamorphosis occurred, the direction of growth was usually downward with the grain of the wood, although 29 specimens of *Teredo bartschi* were not large enough to measure a direction of growth (Table 5, last line).

Table 3. Survivorship, reproduction, and final lengths of *Teredo bartschi* in various temperature-salinity combinations. Two panels per combination. N = initial numbers per wood panel.

Experimental Conditions		Mean Length (mm)	± S.D.	N	Percentage Mortality	Date of first Reproduction
30°	22 ‰	37.45	15.36	48	15%	Apr. 27
		24.20	10.24	75	8%	Apr. 27
	14 ‰	37.23	10.10	31	42%	Apr. 27
		23.96	8.61	75	25%	Apr. 27
	6 ‰	26.00	9.94	53	15%	May 11
		9.85	4.41	61	69%	—
20°	22 ‰	37.25	15.18	12	8%	Apr. 8
		14.76	5.63	164	0	Apr. 14
	14 ‰	11.09	5.96	44	0	May 11
		14.98	5.64	105	0	May 5
	6 ‰	13.55	7.15	31	0	—
		17.07	8.18	53	0	May 11
10°	22 ‰	4.90	3.06	74	20%	—
		4.24	2.14	17	18%	—
	14 ‰	4.84	2.74	83	53%	—
		2.67	0.58	20	85%	—
	6 ‰	3.22	2.37	50	32%	—
		4.16	3.34	25	40%	—

Table 4. Wood Preferences, *Teredo bartschi* Pediveligers. Sample size is 10 per trial.

	Trial 1	Trial 2	Trial 3	Trial 4	Total
New Wood:					
On Wood	7	6	6	6	25
Swimming	1	0	2	0	3
Lying on glass	2	4	2	4	12
Old Wood with no adults:					
On Wood	0	0	0	2	2
Swimming	4	4	6	5	19
Lying on glass	6	6	4	3	19
Old Wood with adults:					
On Wood	0	0	2	1	3
Swimming	10	6	4	4	24
Lying on glass	0	4	4	5	13

Table 5. Settlement patterns, teredinid species. The data are numbers of individuals.

	Settlement:		Growth:		Borehole Within 10 cm of mudline:	
	exposed	against bulkhead	up	down	yes	no
1980 (4 mo.)						
T. navalis	3	6	2	7	3	6
T. bartschi	5	9	3	11	13	1
1981 (16 mo.)						
T. navalis	4	3	2	5	1	6
T. bartschi	53	26	15	35	0	79

SEASONAL SETTLEMENT

The limited number of plankton samples taken contained no shipworm larvae in June and November, 1980-81. Pediveligers of *Teredo bartschi* were found only within 1 m of bulkheads. They were always common when found, but were found only on two occasions (October, 1980 and July, 1981), and at two of seven stations sampled. Veligers and pediveligers of *T. navalis* were sampled on six occasions, were at more stations (6 of 7), and were found in the samples taken farthest from the bulkheads (2-3 m).

Figure 2 shows the months in which each species taken from panels each month at Oyster Creek and Forked River contained mature larvae in the brood pouch. Figure 3 shows the months in which successful settlement on new panels occurred. These data can be compared against monthly temperature and salinity records for Oyster Creek, Forked River, and control stations (Figs. 4 and 5). Bay controls are stations on the bay, north and south of the thermal effluent area of Oyster Creek, which extends north from Oyster Creek to Forked River and south to Waretown (Fig. 1). Creek controls are stations 3 and 7 inside tidal creeks, representing salinity variation in tidal creeks without the influence of the power plant pumping activity. In every month, adult *T. bartschi* were brooding larvae, whereas none were found in *T. navalis* during January-March. The brooded larvae of *T. bartschi* failed to settle successfully during winter, but settlement was prolonged compared to the native species.

DISCUSSION

SALINITY

It is well-known that salinity affects growth, respiration, and filtration activity of bivalves (Böhle, 1972; Shoemaker, 1973; Van Winkle, 1968). Results reported here are close to those of Blum (1922), who found for adults of *Teredo navalis* a minimum salinity for survival of 6-8 $^0/_{00}$. Hoagland (1983b) found that adults of both species could remain active between 7-45 $^0/_{00}$ at 24^{0}C. These experiments confirm the assertion that bivalve larvae are less tolerant than adults of extremes in salinity. The upper salinity tolerances of these teredinid juvenile stages are far less than those of adults, although lower tolerances are similar.

The difference between adults and larvae of *Teredo bartschi* in lower salinity tolerance was not as great as might be expected, based on the ability of the adult to close off its burrow with its pallets. The upper salinity tolerance was not limiting to adults or pediveligers in the study area of Barnegat Bay, but might be in intertidal tropical mangroves. It may appear that salinity is not a factor limiting distribution of *T. bartschi.* However, under natural conditions, the *T. bartschi* larvae live closer to their lower salinity limits (6-7 $^0/_{00}$) than to their upper limits (35 $^0/_{00}$). Specimens of *T. bartschi* do not grow well and show decreased activity below 10 $^0/_{00}$; this fact is compatible with their distribution in Oyster Creek and lower reaches of Forked River. *Teredo bartschi* have been found in waters that reach salinities of 7.5-30 $^0/_{00}$, but rarely go below 12 $^0/_{00}$ (Fig. 4). The data suggest that healthy, stable populations of *Teredo bartschi* will not exist if salinity remains below 7 $^0/_{00}$ for a considerable time.

Teredo bartschi's ability to tolerate low salinities temporarily is also clear from experiments on sudden salinity change. As in any wild population, there is considerable variation in salinity tolerances among individuals. Wide salinity tolerances of *T. bartschi* enable it to live in estuaries (including mangroves) where sudden but short-term changes in salinity are common due to hurricanes and other natural factors. Rising salinity causes a more instantaneous response in larvae than does falling salinity. It evokes a protective response of closing the shell. Larvae at salinities of 6-7 $^0/_{00}$ or less exhibit gaping, which is probably due to swelling of tissues from failure of osmoregulation. Greater boring activity in *Teredo bartschi* at 10-15 $^0/_{00}$ may increase the probability that the animals will settle at a portion of the estuary optimal for survival.

TEMPERATURE

Failure of pediveligers of *Teredo bartschi* to settle and bore at temperatures below 16^{0}C limits the reproductive period of the species in northern waters, even though larvae can be found in the brood pouches of adults nearly year-round (compare Figs. 2 and 3). Based on temperature alone, one would expect reproduction, larval development and settling in Barnegat Bay, N.J. to occur from sometime after early April to mid-November for *T. navalis* and from about May to late October for *T. bartschi* (Figs. 4, 5). In reality (Fig. 3), *Teredo navalis* settles over a narrower period (late May-early November), and *T. bartschi* occasionally settles as early as April and as late as November. In Florida, *T. bartschi* settles year-round.

The temperature range of *Teredo bartschi* is shifted about 5^{0}C higher than that of *T. navalis*, as expected for a subtropical versus a temperate-zone species. Adults have wider tolerance limits than juveniles because they can survive much lower temperatures than larvae; in experiments parallel to those reported here for juveniles, *T. bartschi* became inactive at 13-17^{0}C while *T. navalis* became inactive at 3-4^{0}C; death occurred at $\sim$3^0 and 0^{0}C, respectively (Hoagland, 1983b). Upper temperature limits were similar for larvae and adults.

In Oyster Creek, the upper limit temperature is reached or slightly exceeded in summer, but only for short periods. In winter, even in the thermal effluent, water temperature falls below the minimum for *T. bartschi.* Indeed, heavy mortality did occur every winter for this species, leading me to suspect that strong selection for lower temperature tolerance was occurring. Another possibility was that there was an additional point source of heat entering Oyster Creek, raising the temperature locally. Warm water was found to be entering Oyster Creek from homes near one station, but winter temperature at that point was still only 2-3^{0}C, not appreciably above the temperature of the effluent.

Temperature-salinity experiments showed that minimum temperatures and salinities exist (about 6 $^0/_{00}$ and 10^{0}C) for maturation of *Teredo bartschi* pediveligers regardless of other parameters. Optimal conditions cover a broad range, however. As expected, higher temperature allows more rapid maturation if food is available.

SETTLEMENT

The most surprising result was that involving wood preferences. The common wisdom has been that shipworms settle near the mud line and that they prefer old to newly submerged wood. No aggregation near the water line was detected in the two species examined in this paper, and more settlement occurred on new wood. Attraction to adults did not occur, as it does in some other mollusks.

The limited data on plankton in Barnegat Bay indicate that the presence of pediveligers of *Teredo bartschi* in water is transient and patchy, compared with native species. Although Lane, Tierney, and Hennacy (1954) reported a pediveliger period for this species of only 4 days, it can last four times as long. This is not unusual for long-term brooding species (Turner and Johnson, 1971). The larval stage of teredinids is important as a means of dispersal, not just for feeding, because adults destroy their substratum. *Teredo bartschi* is more patchily distributed than species with planktonic

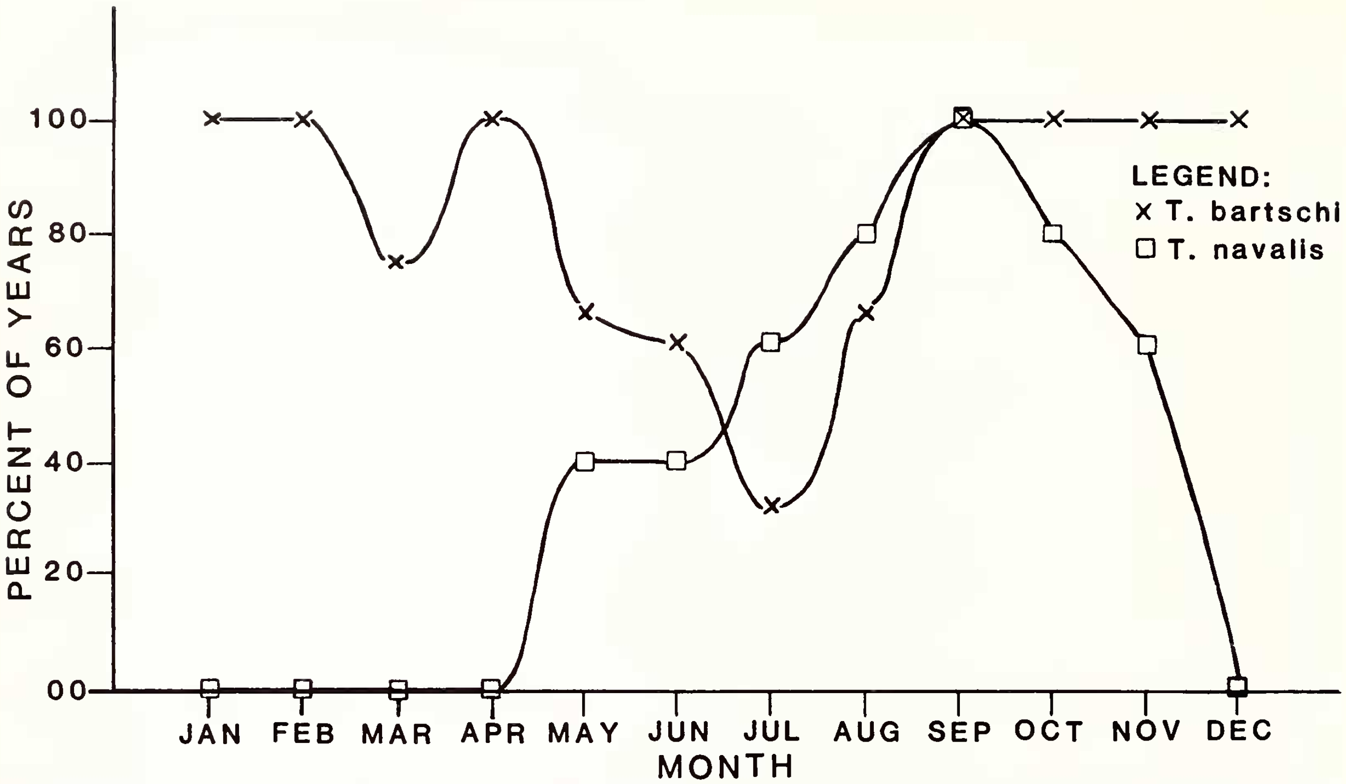

Fig. 2. Percentage of years when mature larvae were present in the brood pouches of *Teredo* species in a given month. The data are for Oyster Creek and Forked River between 1976 and 1982.

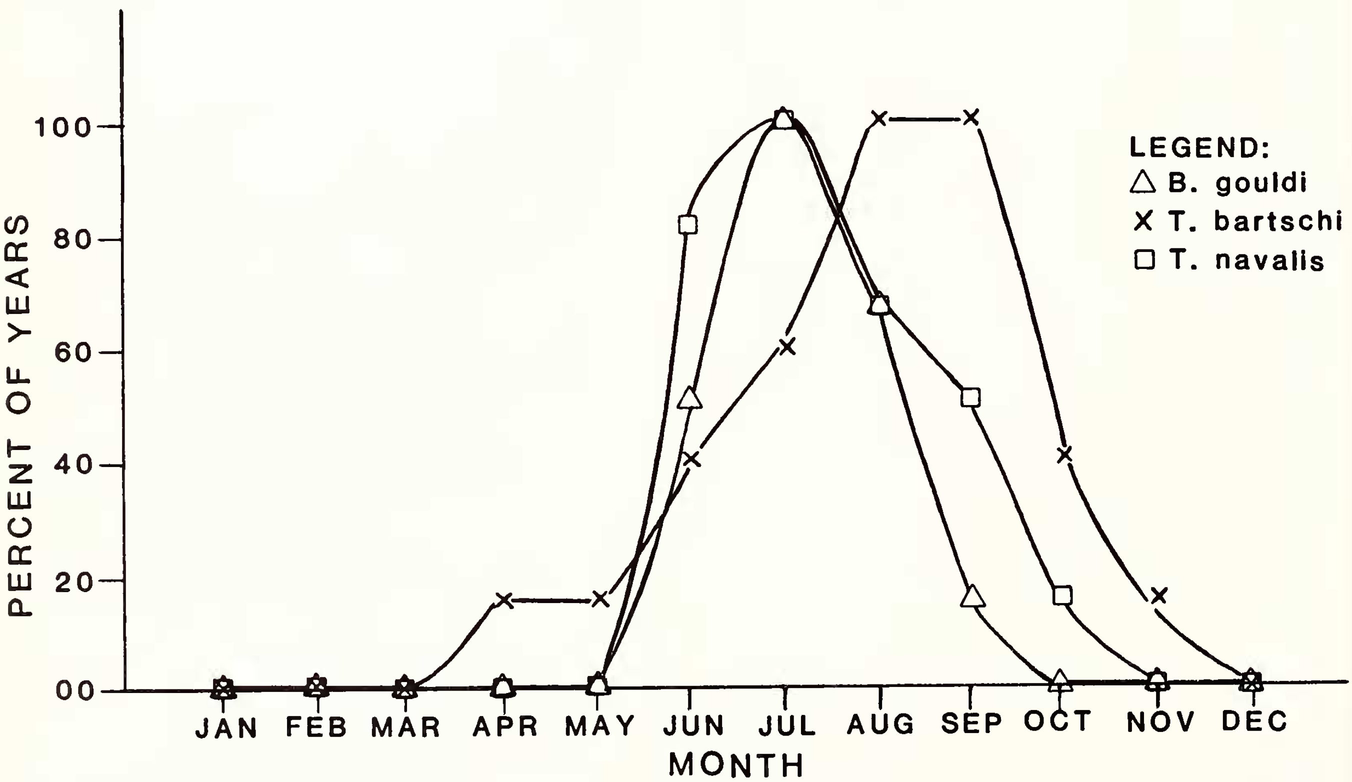

Fig. 3. Proportion of years in which larvae were found settling and boring into wood in a given month. The data are for two *Teredo* species and *Bankia gouldi* in Oyster Creek and Forked River between 1976 and 1982.

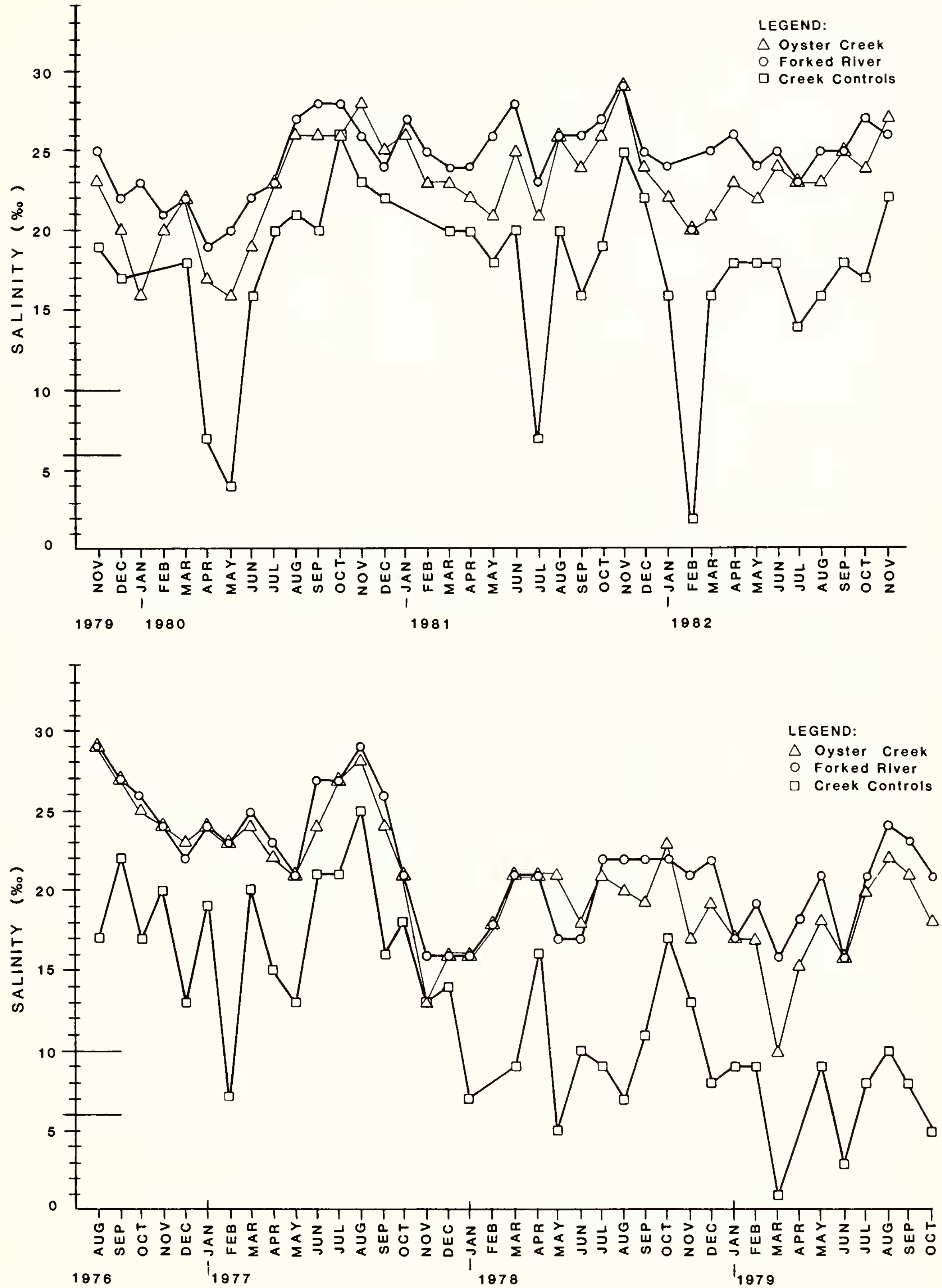

Fig. 4. Averages of monthly salinities in Oyster Creek, Forked River, and control stations, 1976-1982. Bars on y-axis are lower limits for survival (lower bar) and for activity (upper bar) of *Teredo navalis* and *T. bartschi.*

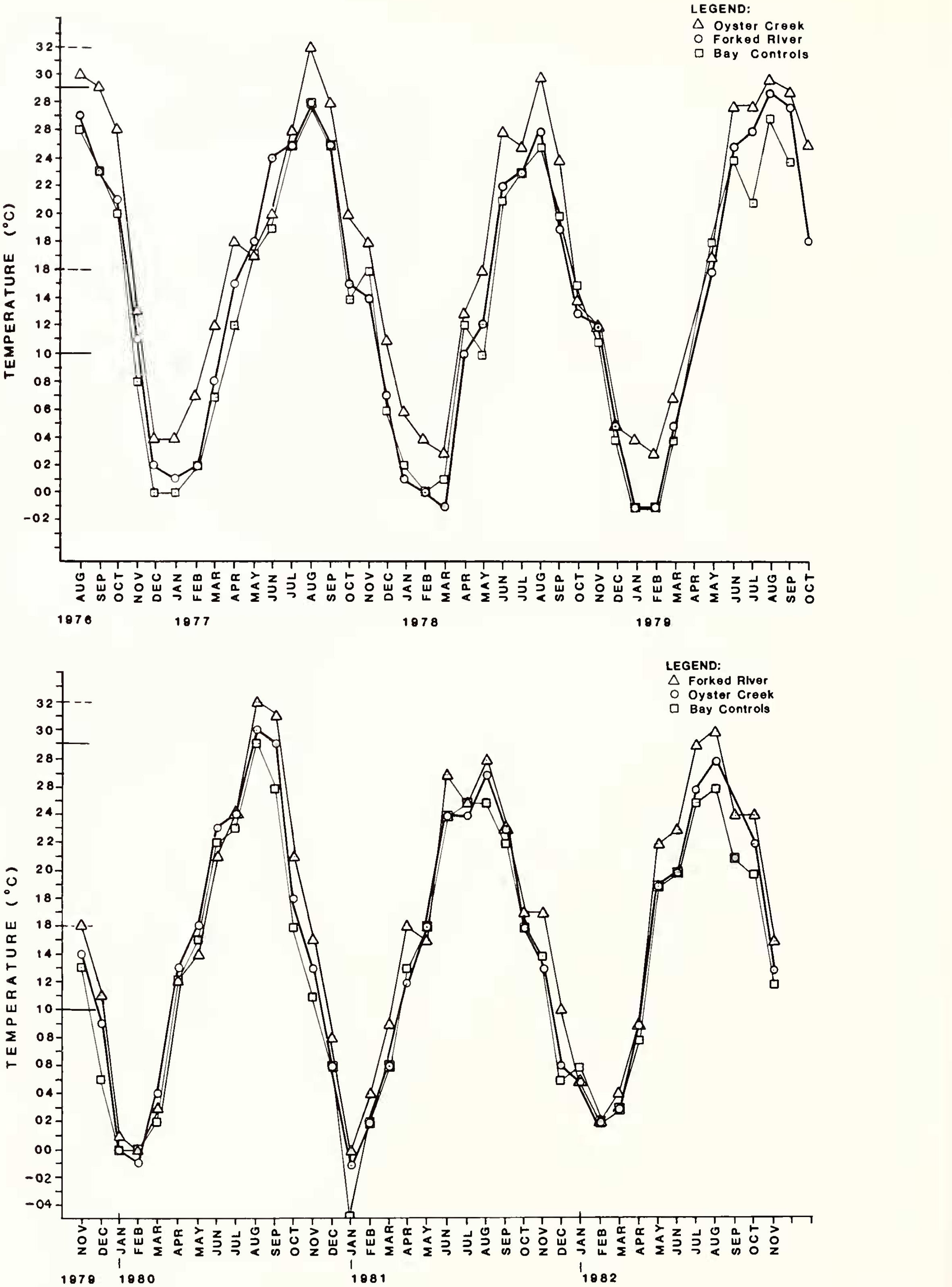

Fig. 5. Averages of monthly temperatures in Oyster Creek and control stations, 1976-1982. Bars on y-axis represent upper and lower limits for reproduction and settlement, *Teredo navalis* (————) and *T. bartschi* (— — — —).

veligers such as *T. navalis*. Most cool-temperature-zone shipworms are released as veligers. Perhaps this is because longer-range dispersal is required where wood is a less concentrated resource than in the mangroves of warmer estuarine waters.

Another conclusion is that the presence of larvae in the gill of *Teredo bartschi* is not indicative of the effective reproductive season in which larvae are successfully released. Nonetheless, the long period over which larvae can be found is another indicator of the flexibility of the species; if temperature and salinity are appropriate, maturation and release of larvae can occur. It is probably this flexibility in timing of larval development, plus the dispersal capabilities of larvae and adults (e.g. in drifting wood) and the likelihood of dispersal of a female with young, which allow *Teredo bartschi* and other teredinids to be such successful introduced species.

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